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Research article

Forest conservation and land development in Puerto Rico

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Abstract

In the Caribbean island of Puerto Rico, rapid land-use changes over the past century have included recent land-cover conversion to urban/built-up lands. Observations of this land development adjacent to reserves or replacing dense forest call into question how the changes relate to forests or reserved lands. Using existing maps, this study first summarizes island-wide land-cover change between 1977-78 and 1991-92. Then, using binomial logit modeling, it seeks evidence that simple forest cover attributes, reserve locations, or existing land cover influence land development locations. Finally, this study quantifies land development, reserve protection and forest cover by ecological zone. Results indicate that 1) pasture is more likely to undergo land development than shrubland plus forest with low canopy density, 2) forest condition and conservation status appear unimportant in that development locations neither distinguish between classes of forest canopy development nor relate to forest patch size or reserve proximity, and 3) most land development occurs in the least-protected ecological zones. Outside the boundaries of strictly protected forest and other reserves, accessibility, proximity to existing urban areas, and perhaps desirable natural settings, serve to increase land development. Over the coming century, opportunities to address ecological zone gaps in the island's forest reserve system could be lost more rapidly in lowland ecological zones, which are relatively unprotected.

Introduction

In many parts of the world, economic shifts away from agriculture lead to forest-cover increases. Increases in urban/built-up lands, subsequently referred to here as *land development,* have occurred more recently on previous agricultural lands. Some of this land development occurs where agricultural lands have already reverted to forest. Urban expansion brings with it concerns over loss of agricultural or forest lands and associated wildlife, loss of cultural or aesthetic values (Beier 1993; Kucera and Barrett 1995; Levia 1998; Yeh and Li 1999; López T. et al. 2001; Schneider and Pontius 2001; López E. et al. 2001), reductions in timber supply (Barlow et al. 1998), impacts on water resources or quality of life (Gersh 1995), and other consequences of urban sprawl (Ewing 1994). Understanding these past and likely future land-cover changes, and their effects on ecological systems, is necessary for the sustainable management of affected ecosystems (Lubchenco et al. 1991; Christensen et al. 1993; Thomas 1996). Such knowledge permits planning that is crucial for landscapes undergoing rapid change (Beier 1993).

Landscape-level planning to minimize critical habitat losses (Scott et al. 1993; Kucera and Barrett 1995; Sanjayan et al. 2000; Eeley et al. 2001) should benefit from recent work to identify important factors in land development (Bockstael 1996; Levia 1998; Yeh and Li 1999; López E. et al. 2001). Scientists are also predicting locations of future such change (Wear and Bolstad 1998; Bradshaw and Muller 1998;

Theobald and Hobbs 1998; Kline et al. 2001; Irwin and Geoghegan 2001; Schneider and Pontius 2001). This work generally supports an explanation of land-use allocation in which location and returns from land development relative to other land uses drive land development likelihood. Higher rents from agriculture or forestry negatively influence land development in western Oregon, for example, as does topography that increases conversion costs (Kline et al. 2001). Existing urban areas exhibit a positive influence on conversion likelihood, for urban proximity presumably increases land values. Although few studies address the topic, existing land cover or its patterns can influence land development in other ways as well. In the United States state of Maryland, for example, lands undergoing residential development have higher property values when large proportions of preserved open space or pasture surround them (Bockstael 1996).

In the Caribbean island of Puerto Rico, the focus of this study, rapid and diverse land-cover changes over the past century initially included large-scale forest conversion to agriculture, which has occurred more recently in other tropical regions (Sader and Joyce 1988; Rudel and Horowitz 1993; Skole and Tucker 1993; FAO 1993). Forest cover in Puerto Rico reached a low of about 6% in the in the late 1940s (Franco et al. 1997). Widespread forest recovery followed as non-farm labor, emigration from rural to urban areas, and immigration to the United States mainland increased. In particular, coffee growers with small land holdings, especially those with land in the least productive areas, apparently sought off-farm income (Rudel et al. 2000). Forest cover increased to about 32 to 42% of the island's area by 1990 (Birdsey and Weaver 1987; Franco et al. 1997; Helmer et al. 2002). The shift toward an industrial- and service-dominated economy in Puerto Rico has recently led to rapid urban expansion (Lopez T. et al. 2001).

As in the eastern United States and Western Europe, newly developed lands in Puerto Rico have lower elevation and slope, and they occur closer to existing urban areas and roads (López T. et al. 2001). Within metropolitan areas, built-up lands may even replace vegetation remaining in locations that are difficult to develop. This study, however, explores factors beyond those commonly associated with land development. It seeks evidence that influences on locations of land development might include forest *ecological integrity* (Karr 1992; Gascon and Lovejoy 1998), land cover, or proximity to protected areas. Observations in Puerto Rico of land development occurring adjacent to reserves or replacing dense forest (Thomlinson and Rivera 2000; Ramos González 2001) call into question whether surrounding undeveloped or reserved lands influence land development, as in the Maryland example mentioned above.

In this study, ecological integrity is measured in terms of forest patch size and canopy development, because the Puerto Rican landscape consisted mainly of closed forests prior to western colonization (Wadsworth 1950). Although many vertebrate species in Puerto Rico have a wide range of habitats including disturbed ones (Cox and Ricklefs 1977), others appear limited to closed forest. The only two studies that have related forest patch size to other ecological data in Puerto Rico have shown that 1) lizard species richness increases with forest patch size (Genet 1999) and 2) large forest patches have a small but positive effect on tree species richness of nearby recovering forest (Chinea and Helmer 2003). We know that edge effects are greater in smaller forest patches and degrade habitat for forest-dependant species in other forested landscapes (Robinson et al. 1995; Gascon and Lovejoy 1998). Two classes of forest canopy development provide a second indicator for ecological integrity in this study. The first class represents early forest succession and includes shrubland and forest with low canopy density; the second class is dense forest. As young forest stands in Puerto Rico age and accumulate basal area, their canopies close, and tree species diversity, number of native tree species, and forest carbon stocks increase (Aide et al. 1996; Rivera and Aide 1998; Chinea and Helmer 2003; Lugo and Helmer 2004).

Although the attributes of forest ecological integrity are debatable, characterizing the influence of a landscape and its forests on land development should enlighten sustainable management at landscape scales. Rapid land-use changes in Puerto Rico require that we address such issues. To this end, my objectives are to use existing data to 1) summarize land-cover changes island-wide between 1977-78 and 1991-92, 2) test, using a binomial logit model of land development, whether land cover, reserve proximity, or simple indicators of forest ecological integrity, including forest patch size or woody canopy development, may influence land development locations, and 3) compare the distributions of land development to the distributions of natural reserves and protected forest in the context of ecological zones.

Table 1. Overlays and class generalizations for land-cover change summary. The summary of areas in Table 3 does not show areas of mixed classes that were disaggregated with the proportions shown in the first column of this Table

Class for land-cover change summary 1977-78 to 1991-92	Classes in 1977-78	Classes in 1991-92
Urban/built-up	Urban/built-up (includes high- and low-density urban/built-up lands)	1. High-density urban/built-up; 2. Urban/built-up from 1977-78
Pasture	Pasture	Pasture
Agriculture (including sun coffee and active shade coffee)	Agriculture (including coffee)	Agriculture (not including coffee)
Change from agriculture to mixed forest/shrub/coffee classes disaggregated to: 1. Pasture (2.4%); 2. Agriculture (24.3%); 3. Forest (72.7%)	Agriculture in 1977-78 that changed to mixed forest/shrub/coffee classes in 1991-92	1. Mixed sun coffee, active shade coffee, forest/shrub and other agriculture; 2. Mixed inactive shade coffee, forest/shrub and forest
Forest (closed woody vegetation)	1. Very dense, tall, large-canopied forest; 2. Dense, medium-tall, smaller-canopied forest; 3. Low canopy-density forest; 4. Shrubland	1. Forest†; 2. Forest/shrub‡ and woodland/shrubland‡; 3. Shrubland
Forested Wetland	Mangrove (includes *Pterocarpus officinalis* swamp)	1. Mangrove; 2. *Pterocarpus officinalis* swamp
Wetland (Non-forest)	1. Emergent wetland; 2. Salt and mud flats from 1991-92	1. Emergent wetland; 2. Salt and mud flats; 3. Inundated freshwater wetland
Other	1. Water in reservoirs, lagoons, rivers and canals; 2. Coastal sand/rock from 1991-92	1. Water in reservoirs, lagoons, rivers and canals; 2. Coastal sand/rock

†Forest: tree cover $>60\%$.; ‡Forest/shrub and woodland/shrubland: a) 25-60 % cover of trees with distinct canopies and an under story of shrubs, seedlings or saplings, or b) dense shrubland, seedlings or saplings

Methods

Study Area

The island of Puerto Rico (17°45' N 66°15' W) is the smallest of the Greater Antilles and with its outer islands encompasses about 8,900 km^2. Ecological zones that support moist broadleaf evergreen forest cover the greatest proportion of the island, but its forests also include dry, wet, rain and lower montane wet and rain forests (*sensu* Holdridge 1967; Ewel and Whitmore 1973). The island's forests have developed over alluvial, sedimentary, volcanic, limestone (including regions with pronounced karst topography) and serpentine substrates, and its forested wetlands include various mangrove communities, *Pterocarpus officinalis* swamps, and swamps in limestone sinkholes. Extensive hydric soils in alluvial plains presumably supported emergent or forested wetland prior to their agricultural use (Lugo and Brown 1988).

Overview of Approach

To begin, I used existing maps of land cover to summarize island-wide changes between 1977-78 and 1991-92. Next, I developed a baseline binomial logit model of land development between 1977-78 and 1994, which included statistically significant variables that commonly relate to land development. The baseline model allowed testing whether land cover, forest indicators, or reserve location might further influence such change. Finally, an analysis of land development trends relied on quantifying land development and protected upland woody vegetation by ecological zone.

Land-cover summary

The summary of land-cover changes used an aerial photo-based map of land cover in 1977-78 (Ramos and Lugo 1994), in which interpreters digitized polygons at a 1:24,000 scale. A map of forest type and land cover, described in Helmer et al. (2002), provided data for 1991-92. This map derived from a 30-m pixel-level classification of Landsat Thematic Mapper (TM) imagery dated 1991-92. Because it underwent no resampling, its minimum mapping unit is probably about 3-5 pixels and <0.5 ha. Comparing the two maps required a geographic information system (GIS) to 1) rasterize the polygon-level map from 1977-78 to a 30-m cell size, 2) co-register the two maps, 3) edit both maps to a comparable set of classes through overlays and class generalizations (Table 1), and 4) cross-tabulate the number of pixels of each class in 1977-78 that changed or did not change to each 1991-92 class. The cross-tabulation used the Summary function in ERDAS Imagine (ERDAS, 1999), which yields a change matrix. Because aerial photos from 1977-78 were not accessible, a validation of the change summary was not possible.

Edits to both maps to improve their comparability included an overlay from the 1991-92 map onto the 1977-78 map of 1) coastal sand/rock, which the earlier map grouped with built-up lands, and 2) some seasonally flooded wetlands that the earlier map grouped with water. The edits also included an overlay of urban areas in 1977-78 onto the map from 1991-92. This step made low-density urban areas, which the map from 1977-78 included with urban/built-up lands, more comparable with the map from 1991-92. In 1991-92, mixed pixels in these areas were often mapped from the Landsat imagery as pasture/grass. Furthermore, the map from 1977-78 included in its urban/built-up class development along generally forested rural roads that the satellite image classification did not detect.

Class generalizations (Table 1) enabled forest cover comparison through combining woody vegetation classes within each date to one class of forest, with the exception of two mixed classes that underwent separate tracking as described further below. Combining these woody vegetation classes into one forest class was reasonable because most woody vegetation in each map had $> 60\%$ woody vegetation cover and would be definable as closed forest on maturity (Helmer et al. 2002). The two mixed classes in the map from 1991-92 were mainly secondary forest, but they were mixed with either sun coffee plus active shade coffee (the first class), or inactive shade coffee (the second class). Separately tracking these two mixed classes allowed quantification of change from the generalized agriculture class in 1977-78, which grouped coffee with non-woody agriculture, to these mixed classes. Subsequent distribution of the mixed class areas among land covers in 1991-92 used estimated proportions of pasture, active coffee cultivation (agriculture), and inactively cultivated plus non-cultivated woody vegetation (forest) that each mixed class contained. The proportions were estimated with accuracy assessment data from the 1991-92 map (Helmer et al. 2002).

Logistic land development model

The binomial logistic regression model of land development had the form:

$$Ln[(\mathrm{Pr\,.\,LD})/(\mathrm{Pr\,.\,ND})] = \beta_0 + \beta_1 X_1 \cdots + \beta_n X_n \tag{1}$$

Where (Pr. LD) and (Pr. ND) are probabilities (Pr.) that a non-urban/built-up cell in 1977-78 underwent land development (LD) or did not undergo land development (ND).

Backward variable elimination determined which spatial variables, of several that commonly relate to land development (Table 2), best explained land-cover change to urban/built-up for a baseline model. These variables included distances to roads, urban areas, large urban areas, and the coastline, along with elevation, slope, aspect, generalized geology and Holdridge life zone. The baseline predictor variables also included gravity indices that, through direct proportionality with urban area size and indirect proportionality with distance from a city, integrate the combined influence of city size and proximity on land development likelihood. The Puerto Rico population census aggregates estimates by municipality and does not reliably estimate population sizes within urban areas. Consequently, whereas human settlement size proxies for human population levels (Tobler 1969), the gravity indices used urban patch size in place of population size. After Kline et al. (2001), a gravity index (Equation 2) first gauged which urban areas had the most potential influence on each observation:

$$\text{Gravity index} = \text{urban patch size} \times \text{distance}^{-2} \tag{2}$$

In Equation 2, urban patch size in ha derived from a contiguity analysis of urban/built-up lands in 1977-78, and distance was proximity in km to a given urban patch. The index was calculated for each observation for each of the island's five largest urban areas (1,000 to 22,000 ha) and for each of two smaller size classes (500-749 and 750-999 ha). Urban areas ≥ 500 ha comprised 44% of all urban/built-up lands in 1977-78. The calculation used average patch size and smallest distance to a patch within that size class for the two size classes. Gravity index sums in Equations 3 through 6 below then derived from using the

Table 2. Variables included in binomial logit model of land development. Discrete variable names are given in the second column.

Variable	Description
Base model	
URBDIST	Distance in km to nearest urban/built-up land in 1977-78 of all sizes.
URBDIST2	Distance in km to nearest urban/built-up areas ≥ 500 ha in 1977-78.
COASTDIST	Distance in km to nearest marine coastline.
PRIMDIST	Distance in km to nearest primary road.
SECONDDIST	Distance in km to nearest secondary road.
TERTDIST	Distance in km to nearest tertiary road.
ROADDIST	Distance in km to nearest primary, secondary or tertiary road.
ELEVATION	Elevation in m.
PCTSLOPE	Percent slope.
Geology1	Geology of substrate, including alluvial, volcanic (base case), karst, and serpentine
Geology2	Geology of substrate, including non-alluvial (base case) vs. alluvial
Life Zone	Holdridge life zone, including subtropical dry, moist, wetrain (wet or rain), and lowermont (lower montane wet or rain) forest.
Gravity indices[1]	
$\mathrm{SIZE{\cdot}DIST}^{-2}$	$\mathrm{ha{\cdot}km}^{-2}$
$\mathrm{SIZE{\cdot}DIST}^{-1}$	$\mathrm{ha{\cdot}km}^{-1}$
$\mathrm{SIZE{\cdot}DIST}^{-0.5}$	$\mathrm{ha{\cdot}km}^{-0.5}$
$\mathrm{SIZE}^{0.5}{\cdot}\mathrm{DIST}^{-1}$	$\mathrm{ha}^{0.5}\cdot\ \mathrm{km}^{-1}$
Land cover, reserve and forest indicator variables	
STATEDIST	Distance in km to nearest Commonwealth reserve in 1980.
FEDDIST	Distance in km to nearest Federal reserve.
PROTDIST	Distance in km to nearest Commonwealth, Federal or private reserve land.
FORSIZE	Size of forest patch in ha.
CNFPROCL	Presence within or outside of the Caribbean National Forest (CNF) proclamation area.
Landcov1	Land cover in 1977-78, including forest1 (very dense, tall, large-canopied forest+dense, medium-tall, smaller-canopied forest), forest2 (shrubland+low canopydensity forest), agriculture, pasture, wetland, other
Landcov2	non-pasture (base case) vs. pasture
Landcov3	woody (base case – forest1 + forest2) vs. non-woody vegetation
SFOREST1, SFOREST2, SWOODY, SPASTURE, SURBAN, SAGRIC	Percent of given land cover in 7.8 ha surrounding an observation

[1] *Gravity indices*Calculated using contiguous urban area size in ha. Each represents a sum of urban patch size divided by distance, with indicated power coefficients, for three urban patches with most potential influence on an observation

size and proximity of urban patches (i = 1 to 3) that yielded the three largest results in Equation 2:

$$\mathrm{SIZE} \times \mathrm{DIST}^{-2} = \sum_{i=1}^{3} \text{urban patch size}_i^{0.5} \times \text{distance} \tag{3}$$

$$\mathrm{SIZE} \times \mathrm{DIST}^{-1} = \sum_{i=1}^{3} \text{urban patch size}_i \times \text{distance} \tag{4}$$

$$\mathrm{SIZE} \times \mathrm{DIST}^{-0.5} = \sum_{i=1}^{3} \text{urban patch size}_i \times \text{distance} \tag{5}$$

$$\mathrm{SIZE}^{0.5} \times \mathrm{DIST} = \sum_{i=1}^{3} \text{urban patch size}_i \times \text{distance} \tag{6}$$

Response data for the model derived from López T. et al. (2001), who screen-digitized developed areas that were new since 1977-78 in SPOT satellite imagery dated 1994. The newly developed areas in this data include two patches where limestone extraction expands into forested land. These data were more suitable for a change model than the Landsat-derived data from 1991-92. First, they were polygon-level interpreted, like the aerial photo-based data from 1977-78. Second, they more accurately mapped low-density urban areas. After rasterizing data from 1994 to a 30-m cell size, a random sample of 5,000 cells not already urban in 1977-78 yielded observations for the binomial logistic regression model of land development likelihood. Existing literature does not evaluate the effects of sample number or density on similar analyses, except with reference to the potential effects of spatial autocorrelation between observations. The 5,000-cell sample covered 0.05% of the entire landscape, which is at the smaller end of the range of sample numbers and densities from other studies. The conservative sample size and its random configuration were intended to minimize autocorrelation effects while adequately sampling change. To further minimize any bias from spatial autocorrelation between observations, a separate spatial analysis excluded 1,088 observations with spacing closer than a distance that takes into account the spatial structure of the land development process (Helmer 2000; Schneider and Pontius 2001). Seventy-five percent of all new land development patches were ≤ 7.8 ha, and a circle of that area would have a radius of just over 150 m. Consequently, I assumed that a radial distance of 150 m would avoid over-representation of small patches while permitting the statistical model to account for variation in explanatory variables within larger patches. Of the remaining observations, 172 had undergone land development.

After developing the baseline model, forward variable selection with backwards elimination evaluated whether additional variables explained variation in land development. These variables included land cover, immediately surrounding land cover, simple indicators of forest ecological integrity (forest patch size or canopy development), or reserve locations (Table 2). Class of forest canopy development derived from generalizing the four classes of upland woody vegetation in the map dated 1977-78 to two classes. The better-developed canopy class, FOREST1, combined the very dense, tall, large-canopied forest class with the dense, medium-tall, smaller-canopied class (Table 1, Table 2). The less-developed class, FOREST2, included low-density forest and shrubland. Reserve location indicators included distance to nearest Federal, Commonwealth or private reserve (forest and non-forest), using a map by Dragoni (2002), and occurrence within the Caribbean National Forest (CNF) proclamation area. Because the likelihood of land development was so small, no attempt was made to use this logistic model to predict future locations of land development (Schneider and Pontius 2001).

Comparison of land development by ecological zone

A map of ecological zones then permitted summary by ecological zone of areas of reserves, upland woody vegetation and protected upland woody vegetation (using the data from 1991-92), and land development (using the data from López T. et al. 2001). Ecological zones were based on climatic zone and geology. They derived from aggregating Figueroa Colon's (1996) GIS overlay of life zone (Holdridge 1967; Ewel and Whitmore 1973) and generalized geology (Krushensky 1995) into zones that represent groups of forest formations and agricultural land uses (Helmer et al. 2002). Multiple regression analyses determined the significance of relationships between zonal percent of island-wide land development and zonal proportion of reserve protection or protected woody vegetation, after accounting for zone area or zonal urban/built-up area in 1977-78.

Results

Island-wide land-cover change

A 64% decrease in agricultural lands of about 119,000 hectares is the largest land-cover change on the island between 1977-78 and 1991-92 (Table 3). About 44,000 ha of this decrease corresponds to an increase in the mixed classes of coffee cultivation and secondary forest. These mixed classes disaggregate on average to 2.4% pasture, 24.3% agriculture (10,635 ha) and 72.7% (31,843 ha) uncultivated woody vegetation (forest). However, the map from 1977-78 includes all coffee cultivation with non-woody agriculture, and that agriculture class probably includes some inactive shade coffee/secondary forest. Consequently, at least a portion of the 31,843 ha forest increase in the coffee-growing region probably represents a classification difference between the two maps rather than actual change. Other agricultural lands change to pasture (~ 48,000 ha), forest (~ 33,000 ha) and urban/developed lands (~ 7,300 ha). Although pasture/grass area increases overall as agricultural lands change to pasture, about 68,000 ha revert to

Table 3. Land cover changes in Puerto Rico, 1977-78 to 1991-92. Data for main island only. The change summary resulted in a smaller total forest area in 1991-92 than that presented in Table 5 because 1) some of the forest mapped in 1991-92 was co-located with urban/built-up lands in 1977-78 (the earlier map included low-density urban/built-up lands and development along rural roads and 2) the map from 1977-78 included more waterways (included in class Other), and mapped them at greater breadths, than the map from 1991-92

	Land cover in 1991-92 (ha)							
	Urban/Built-up	Pasture	Agriculture	Forest	Forested Wetland	Wetland (Non-forested)	Other	Total in 1977-78
Land cover in 1977-78 (ha)								
Urban/built-up	106,961	0	0	0	0	0	0	106,961
Pasture	15,353	170,238	8,338	56,810	281	1,208	627	252,856
Agriculture	7,319	48,094	52,129	77,367	406	1,658	570	187,543
Forest	9,498	68,584	7,139	213,706	339	513	524	300,303
Forested Wetland	362	429	79	1,163	4,541	218	115	6,907
Wetland (Non-forest)	437	1,262	160	604	354	2,633	16	5,467
Other	725	1,572	473	2,129	351	135	6,225	11,610
Total in 1991-92	140,655	290,178	68,319	351,780	6,272	6,365	8,077	
Land cover change: 1977-78 to 1991-92								
Hectares	33,694	37,322	− 119,224	51,477	− 635	898	− 5,386	
Percent	32	15	− 64	17	− 9	16	− 46	

[1]Rasterizing vector data to 30-m cells increased urban/built-up area in 1977-78 by 8.7% from the 98,400 ha that Lopez T. et al. (2001) report. [2] Overlaying the rasterized data for urban/built-up lands from 1977-78 onto the 1991-92 data increased urban/built-up land area by 52% from the 92,800 ha that Helmer et al. (2002) report.

forest. The large decrease in land area classified as “Other” occurs because water in rivers and reservoirs occupies larger areas in the map from 1977-78 than the more recent satellite image-derived map. Although small in total area, a large percentage increase of 16% in non-forested wetlands occurs through creation of new reserves coincidental with inactivation of infrastructure that drained wetlands. The largest extents of land development occur on pasture/grass lands (over 15,000 ha), forested land (~9,500 ha) and agricultural lands (~7,300 ha) (Table 3). Qualitative examination of the maps indicates that these results almost certainly present a valid picture of trends in land-cover change for the island. However, the lack of error assessment in the summary of land-cover change, and methodological differences in developing the two maps, imply unknown uncertainty in estimates of land-cover change.

Attributes of land development

Negative coefficients in the logit model and negative marginal effects coefficients indicate that land development likelihood decreases with distance from any existing development, urban areas ≥ 500 ha, any road, or as elevation or slope increase (Table 4). It is also less likely in alluvial as opposed to non-alluvial substrates. Three gravity indices also explain significant variation in land development likelihood. These indices include $SIZE \cdot DIST^{-1}$, $SIZE \cdot DIST^{-0.5}$, and $SIZE^{0.5} \cdot DIST^{-1}$. The index $SIZE \cdot DIST^{-1}$ has an unexpected negative coefficient in the model. Distance to coast is not significant.

Significant factors in the land development model beyond expected correlates include surrounding woody vegetation with less canopy development (SFOREST2), which decreases land development likelihood, and surrounding pasture (SPASTURE), which increases land development likelihood. Those proportional measures of surrounding land cover generally displace discrete land cover variables in forward variable selection. In the absence of variables for surrounding land cover, only the PASTURE case of Landcov1 has land development likelihood that is significantly different from the reference case of woody vegetation with more canopy development (FOREST1). Insignificant in the model are amount of surrounding woody vegetation with more canopy development (SFOREST1) and presence (Landcov3) or amount of any surrounding woody vegetation (SWOODY). These results indicate that although the

Table 4. Coefficient estimates for explanatory variables for the model estimating the log-odds ratio that non-urban land in 1977-78 is developed in 1994. Marginal effects coefficients describe the probability of conversion at the explanatory value mean. Summary statistics: n = 3912, Log Likelihood = − 577, Restricted Log Likelihood = − 705, χ^2 = 257, d.f. = 12, P < 0.0001. Table 1 contains variable descriptions

Variable	Estimated Coefficient[1]				Marginal Effect				Mean of X[2]
Constant	− 1.3	±	0.6	***	− 0.018	±	0.012	**	
URBDIST	− 2.2	±	0.9	***	− 0.032	±	0.012	***	0.45
URBDIST2	− 0.044	±	0.036	*	− 6.2E-04	±	5.2E-04	*	9.8
ELEVATION	− 0.0033	±	0.0016	***	− 4.7E-05	±	2.2E-05	***	249
ROADDIST	− 3.8	±	2.4	**	− 0.054	±	0.034	**	0.13
SIZE·DIST$^{-0.5}$	7.8E-05	±	4.5E-05	***	1.1E-06	±	7.2E-07	**	5460
SIZE·DIST^{-1}	− 3.0E-05	±	1.8E-05	**	− 4.2E-07	±	2.9E-07	**	4308
SIZE$^{0.5}$·DIST^{-1}	0.0017	±	0.0012	**	2.5E-05	±	1.9E-05	*	46
PCTSLOPE	− 0.023	±	0.016	**	− 3.2E-04	±	2.3E-04	**	23
ALLUVIAL	− 0.57	±	0.42	**	− 0.0081	±	0.0063	*	0.20
SPASTURE	0.0050	±	0.0048	*	7.1E-05	±	6.9E-05	*	30
SFOREST2	− 0.011	±	0.010	*	− 1.5E-04	±	1.5E-04	*	10
CNFPROCL	1.2	±	1.1	*	0.017	±	0.016	*	0.03

[1]Asterisks indicate coefficient *p*values, with ***, **, and * representing, respectively; $p <$ 0.0005; $p <$ 0.005 and $p <$ 0.05; [2]Mean value of explanatory variable or proportion of observations within category for discrete variables

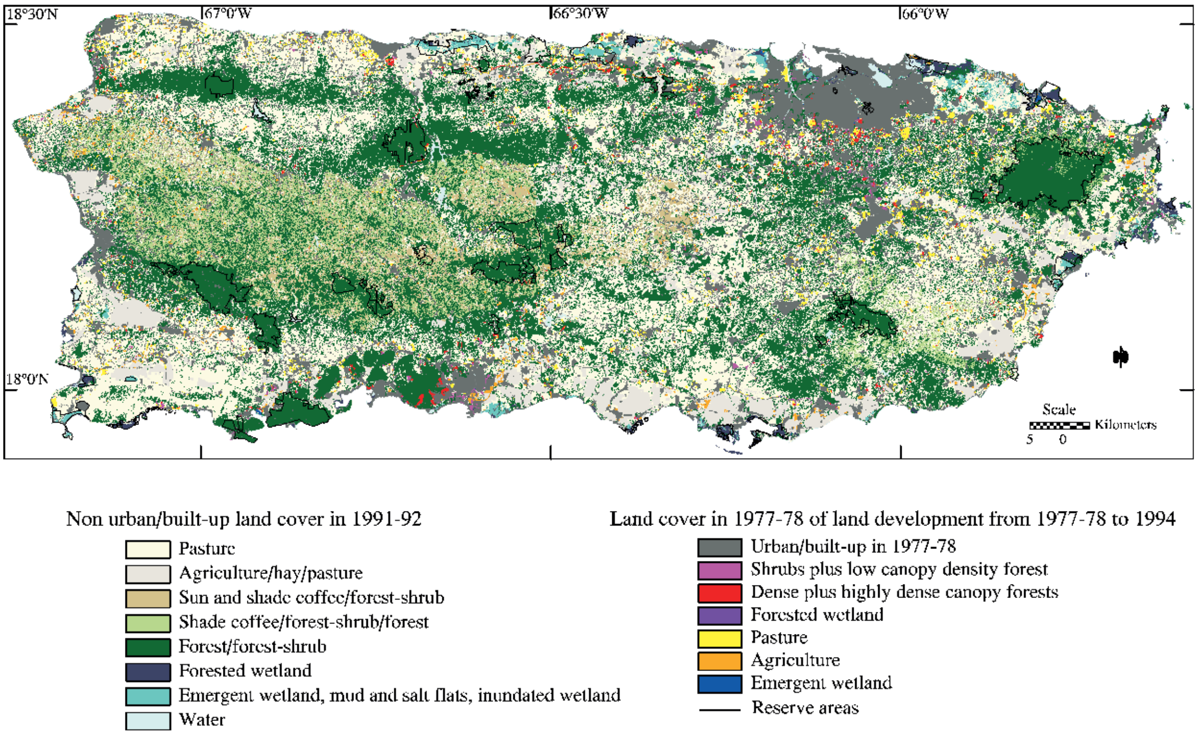

Figure 1. Puerto Rico land cover in 1991-92 (Helmer et al. 2002) including land cover in 1977-78 (Ramos and Lugo 1994) of land development between 1977-78 and 1994 (Lopez T. et al. 2001). Black lines bound Federal, Commonwealth and private reserve areas.

less-developed canopy class undergoes less land development than does pasture, land development does not distinguish between the two canopy development classes.

The other indicator of forest ecological integrity, forest patch size, does not significantly explain variation in land development after accounting for other factors. Among all forested observations, those changing to urban/built-up lands are within forest patches that average 12.4 ha in size. Those not undergoing land development occur in similarly sized patches of 10.7 $\pm$ 6.54 ha. A lack of significant influence on land development also applies to reserve proximity; however, land development is more likely to occur within the boundaries of the CNF proclamation area.

Ecological distribution of land development

The proportions of island-wide land development between 1977-78 and 1991-92 are tiny in the highest elevation ecological zones and zones with relatively non-arable substrates such as serpentine (Table 5). These same areas have the greatest proportions of protected area (25-75%) and protected woody vegetation (24-73%). By contrast, most land development occurs in moist ecological zones over alluvial or volcanic and sedimentary substrates or in the non-serpentine dry zones. These zones have much smaller proportions of protected woody vegetation. In fact, the base 10 logarithm of the percent of island-wide land development within each ecological zone, between 1977-78 and 1991-92, is inversely related to proportion of that zone under protection ($p < 0.005$). This relationship holds even after accounting for either the proportion of island-wide urban/built-up lands already existing within an ecological zone (Adj. R-sq = 0.90) or the total zone area (Adj. R-sq = 0.88). Covariance occurs between these two variables, and they behave similarly in models of land development by ecological zone. Likewise, after accounting for existing urban extent or zone area, the base 10 logarithm of the percent of island-wide land development within each ecological zone relates inversely to proportion of each ecological zone that is protected woody vegetation ($p < 0.001$). Ecological zones with the least amount of protection undergo the majority of land development.

Discussion

The island-wide summary of land-cover changes in Puerto Rico demonstrates three positive natural resource trends between 1977-78 and 1991-92. First, the area of emergent and freshwater inundated wetland substantially increases (16% for the time period), with new reserve designation and subsequent restoration of wetland hydrology on previously drained ag-

Table 5. Areas of ecological zones, zonal proportions of island-wide land development, proportions of each zone under protection, upland non-cultivated woody vegetation within zone, and areas and percentages of each zone that are protected upland woody vegetation

Ecological Zone[1]	Percent of island-wide land development	Zone Area (ha)	Percent of zone protected	Total Upland Woody Area (ha)	Protected Upland Woody	
					Area (ha)	% of Zone
Dry-Alluvial	10.5	45,179	5.5	5,368	211	0.5
Dry-Volcanic/Sedimentary/Limestone	11.8	82,379	4.6	30,441	3,319	4.0
Dry/Moist-Serpentine	1.9	6,411	25.1	3,690	1,517	23.7
Moist-Alluvial	26.0	144,767	4.5	16,224	729	0.5
Moist-Volcanic/Sedimentary	29.0	270,513	0.5	109,699	762	0.3
Moist-Northern Limestone, rainfall $<$1500 mm/yr	3.2	19,988	3.3	6,381	488	2.4
Moist/Wet-Northern Limestone, rainfall $>$1500 mm/yr	3.7	94,127	4.2	53,240	3,746	4.0
Wet/Lower montane wet-Serpentine	0.43	5,107	71.1	4,871	3,541	69.3
Wet-Volcanic/Sedimentary/Alluvial[1]	13.3	187,397	5.8	122,613	10,009	5.3
Rain/Lower Montane Wet or Rain-Volcanic/Sedimentary/Alluvial	0.16	13,288	74.7	12,632	9,705	73.0
Total	100	869,156	5.2	365,160	34,026	

[1]Aggregated from geoclimatic zones in Figueroa-Colón (1996), and based on a geographic information system overlay of Ewel and Whitmore (1973) and Krushensky (1995) (see Helmer et al. 2002)

ricultural lands. Second, forests expand via reversion from pasture or agricultural land, which agrees with results of previous work (Franco et al. 1997; Rudel et al. 2000; Ramos González 2001). Granted, overall species composition of these forests differs from native forest (Zimmerman et al. 1995; Aide et al. 1996; Franco et al. 1997), (as is the case for recovering forest in parts of the United States [White and Mladenoff 1994; Foster et al 1998]), and naturalized and exotic species often dominate this recovering forest (Chinea 2002; Chinea and Helmer 2003; Lugo and Helmer 2004). However, these secondary forests still provide positive environmental services as they accumulate nutrients and species (Brown and Lugo 1990; Lugo and Helmer 2004). A third positive aspect of the island landscape is that forests at the highest elevations and on serpentine substrates, which harbor endemic species with ranges limited to those ecological zones, have substantial portions of their areas protected. Notably, these well-protected zones also have the least agricultural potential and a relatively rugged topography.

The base model of land development generally agrees with known factors that relate to land development, including topographic and locational attributes such as distances to roads or existing urban areas. These findings agree with Lopez T. et al. (2001), who show that newly developed lands have lower elevation and slope and are closer to existing urban areas and roads. The negative influence of alluvial relative to other geology types may reflect a higher agricultural potential of those areas. At the same time, the logit model shows little evidence that ecological integrity of unprotected forest discourages land development. To the contrary, the chances of forest conversion increase within the boundaries of the CNF proclamation area. Although somewhat surprising, the insignificance of reserve proximity confirms other findings. In the municipality of Luquillo, which includes part of the CNF and its proclamation area, 80% of land development from 1988-1993 replaced dense forest (Thomlinson and Rivera 2000). The relatively natural setting there may be more attractive to homebuyers (Thomlinson and Rivera 2000). Ramos González (2001) observes more land development in northeastern Puerto Rico closer to one protected area and unclear relationships between land development and proximity to two others. All else equal, a forest stand may undergo clearing for land development regardless of its extent, canopy development or reserve proximity.

Indeed, the study documents that more land development in Puerto Rico occurs in ecological zones that already have the most urban/built-up area and the least protection. Even after accounting for larger zone area or urban/built-up area, land development relates inversely to zonal proportions of protected area or protected upland forest. This latter analysis only demonstrates a relationship; however, it reveals that forest protection occurs most frequently on lands that are uneconomical to farm or develop, but which also conveniently harbor some endemic species.

To summarize, the likelihood of land development in Puerto Rico balances proximity to and sizes of existing urban areas with topographic factors that probably affect ease and cost of land development, regardless of its landscape-level ecological implications. That balance is visible within the San Juan metropolitan area, where topographic factors may not be important, because forested limestone hills undergo leveling. Lopez E. et al. (2001) notes similar pressures surrounding Morelia City, Mexico. Other factors, such as an attractive natural setting, may also be important. Although land development distinguishes between pasture and shrubland plus low canopy density forest, forest with more developed canopy cover, or large forest patches, do not negatively or positively impact it.

These findings imply that opportunities to address ecological zone gaps in the island's forest reserve system could be more rapidly lost in under- or unprotected lowland zones, such as zones with alluvial soils or in the moist volcanic/sedimentary zone. Sustainable management of ecological systems in complex tropical areas requires some protection of all ecological zones, including connectivity with montane reserve areas. Ample evidence identifies species that require an elevational range for resources, breeding, or post-hurricane refugia in Puerto Rico and elsewhere (Powell and Bjork 1995; Covich and McDowell 1996; Scatena and Johnson 2001; Wunderle 2002).

Assuming that land-use allocation principles continue to favor land development and forest recovery over agriculture and pasture, Puerto Rico can seize the opportunity in the coming century to sustainably direct locations of land-cover change and thereby avoid the potentially high costs of lost opportunities to conserve, restore, or strategically manage ecosystem services provided by lowland areas. Difficulties with designing conservation reserves that span the ranges of migrating species is not a new problem. Yet planning based on such considerations is crucial in

Puerto Rico because its landscape continues to undergo rapid change as it did during the 20th Century.

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